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Pollination experiments with Anonas

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Among the tropical and semi-tropical fruits that have found a congenial home in south Florida are the sugar apple, *Anona squamosa* L., the custard apple, *Anona reticulata* L., and the cherimoya, *Anona Cherimolia* Miller; one species, the pond apple, *Anona glabra* L., is indigenous. The sugar apple was introduced in 1833 by Dr. Henry Perrine, but whether the plants survived after his death in the massacre at Indian Key in 1840, and are the progenitors of the now naturalized plants of this species on the Florida Keys, or whether some of these are the offspring of a later unauthenticated introduction will probably never be known. It is probable that several separate introductions have been made from the Bahamas, where the species luxuriates and with which islands the early settlers on the Florida Keys were in intercommunication. Introductions have probably also been made from Cuba by way of Key West. The custard apple was probably introduced in a similar manner. The cherimoya referred to by Reasoner in Bull. No. 1, Div. of Pomology, U. S. Department of Agriculture, in 1887, is the custard apple, with which the cherimoya is very frequently confounded. The first authentic introduction of the cherimoya was made in 1895, when Mr. William Freeman brought seed to Little River from San José, Costa Rica.

The two first-named species have fruited fairly well in Florida, the sugar apple frequently coming into bearing the third year from the sowing of the seed; but only rarely do the trees bear abundantly. The failure of the cherimoya to set fruit after having bloomed for several years led the writer to begin investigations in 1907, in regard to the probable cause of the sterility of this species in Florida. From the construction of the flowers and their fragrance it became evident that they were entomophilous, and in the course of the observations it was discovered that they were proterogynous. After this discovery was made there was begun a comparative study of the flowers and pollination of the sugar apple and the custard apple, the flowers of which superficially appeared to be identical with those of the cherimoya. It was then found that these two species were likewise proterogynous. In the course of this investigation it was noted that the flowers of the cherimoya and the custard apple shed their pollen in the afternoon from about 3.30 to 6 P.M. In the sugar apple the pollen is discharged in the morning from the rising of the sun to about 9 A.M., when practically all the pollen is shed. After examinations of a large number of trees of this species three were found to shed their pollen in the afternoon and the interesting fact was noted that this phenomenon does not occur on the same trees in the morning. A more limited number of trees of the custard apple and the cherimoya were available for observation; were it extended to a large number it is quite probable that individual trees may be found that shed their pollen at other times of the day than has been noted in the course of these observations.

The flowers of the three species enumerated, belonging to the section *Attae* Martius, are nodding; the calyx is tripartite, the sepals small and triangular; the six petals are arranged in two rows, the three exterior ones being linear-oblong with an obtuse sometimes acute apex; outside, these petals are ferruginous-tomentose and velvety in the cherimoya, while in the custard apple and the sugar apple they are greenish and sparsely hairy. The petals are shortest in the custard apple, being sometimes only 16 mm. long; in the cherimoya they frequently exceed 30 mm. in length. In all species they are keeled inside, whitish, concave, with a maroon blotch in the cavity, at the base; the interior petals are rudimentary; the number of stamens, which are attached to the torus, is indefinite and they cohere by a connective gland beyond the anthers, surrounding the syncarpium in which an indefinite number of carpids are united. As the flowers become full grown a viscid fluid is secreted that covers the syncarpium and which appears to be most abundant about twenty-four hours before the pollen is shed.

Until the shedding of the pollen the petals assume an almost perpendicular position (see FIGURES 1 and 3*a*) and leave a small opening, facing downward, for the entrance of pollen-bearing insects.* (In individual trees of the cherimoya the apical end of of the petal is curved outward, though not to the extent of facilitating the conveyance of pollen to the stigma.) As the time approaches for the discharge of the pollen, the petals spread out and upward so rapidly that the movement is readily perceived; this phenomenon is accompanied by the exhalation from the flower of a fragrance analogous to that of a well-ripened banana or pineapple in the cherimoya and custard apple; in the sugar apple it partakes of the odor of ethyl acetate and continues for a few hours until the pollen is shed, after which it disappears and the petals wither. The fragrance is also noticeable in the flowers twenty-four hours previous to the shedding of the pollen and is undoubtedly intended to serve as a guide for insects that aid in the pollination. The stigma is now readily approached by large as well as small insects and were the stamens and stigmas synchronous self-pollination by insects or the wind might be effected (FIGURES 2 and 3*b*).

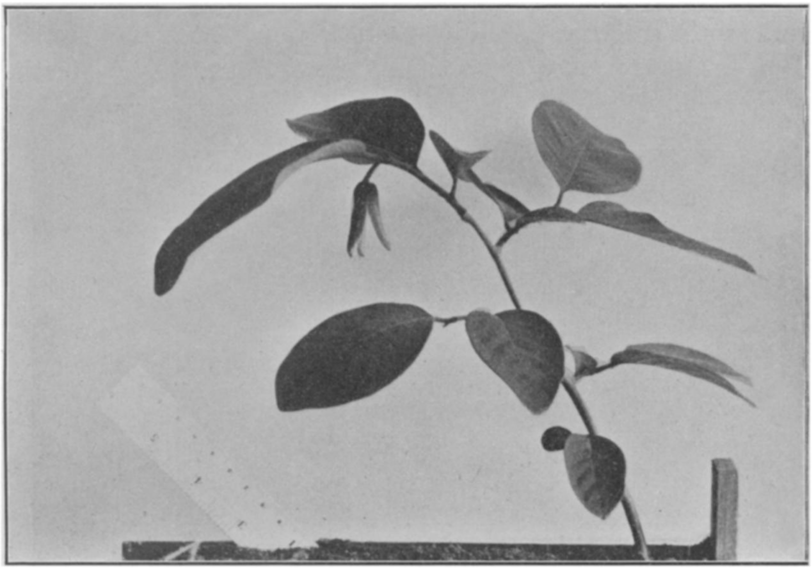

FIGURE 1. Flower of the cherimoya, showing position of petals when the stigmas are in the receptive state. (One third natural size.)

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*This expression is used advisedly, as it is very evident that the flowers are not constructed for wind pollination nor are self-pollinized, as will appear presently.

Owing to the advanced season of the year when the investigation began, with the consequent scarcity of bloom, extensive observations must perforce be suspended until the advent of the flowering season of another year. A small beetle, identified by Dr. C. L. Marlatt, assistant chief of the Bureau of Entomology as *Colastus truncatus*, was then found acting as pollinating agent in considerable numbers in the flowers of the sugar apple. This spring (1910) I found the same insect in flowers of the cherimoya and sent a specimen of this as well as of another species to the Bureau of Entomology for identification. The latter was identified by Prof. F. H. Chittenden as "*Triphleps*, probably *insidiosus*." As this specimen is the only one of this species so far discovered, its presence in the flower may have been accidental. Another small beetle was found in the flowers of the sugar apple and sent to Dr. Marlatt for identification in 1908, who transmitted to me the following notes, by Mr. E. A. Schwarz, in regard to this species:

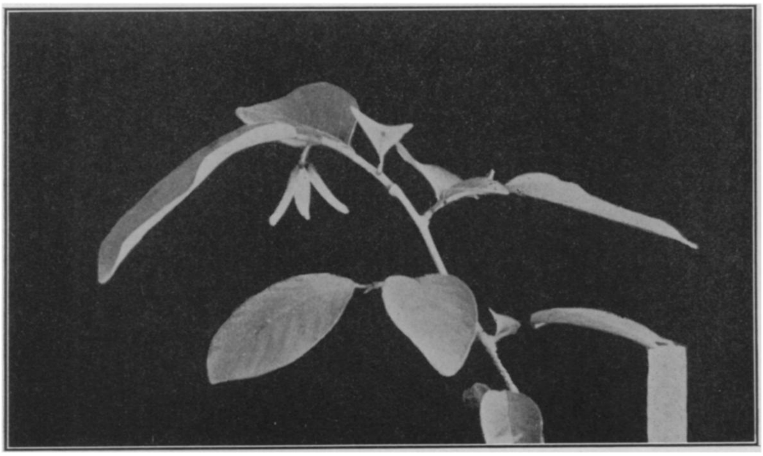

FIGURE 2. The same flower as in Figure 1, 24 hours later, showing position of petals when the pollen is discharged. (One third natural size.)

"The small brownish beetle has for a number of years been represented in our collection, but belongs to a family of Coleoptera which has been very little studied so far, the genus of which has never been determined. As near as we can say it belongs to the group *Pharaxonothi*. Many years ago the species was found by the late Mr.H. G. Hubbard, an assistant of the Bureau, and he made some interesting observations on it at Crescent City, Florida. The larvae were found by him feeding upon the substance of the flower stems of both male and female cones of the coontie plant, *Zamia integrifolia*, but in no way injuring the flower. Mr. Hubbard came to the conclusion that both the larvae and the imagos of this little beetle are intended to facilitate the fertilization of the plant. The same species was found by me in great numbers on the flowers of the Florida palmetto and no further notes have been taken by me. The species does not seem to occur in the West Indies, nor is anything similar reported from Central America. There are various genera of the family described from South America but whether or not this species is identical with any one of them can not be ascertained at present."

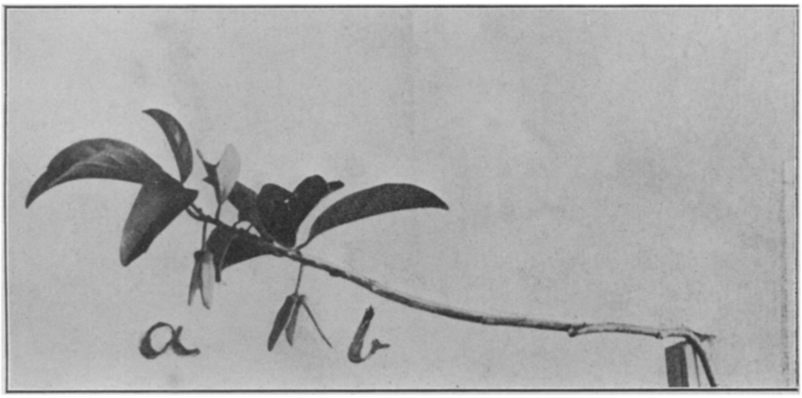

FIGURE 3. Flowers of the sugar apple; *a*, when the stigmas are receptive to the pollen; *b*, at the time of the discharge of the pollen. (One third natural size.)

In addition to these species a small thrips frequents the flowers of these Anonas and probably to some extent assists in their pollination.

In order to ascertain the validity of the theory of proterogyny in the Anonas in question a series of pollination experiments was inaugurated in 1908 on all three species, which was concluded this spring. In the course of this experiment on a cherimoya tree pollen was applied to the stigmas of twenty-seven flowers at the time of the discharge of the pollen in the flower, all of which dropped. The pollen was in some instances taken from the flower pollinated, in others from other flowers of the same tree. In a few instances pollen of the sugar apple and the pond apple was applied. Thirty-four flowers were pollinated twenty-four or more hours before the shedding of the pollen and all set. Many of these dropped after partial development but the dissection of the immature fruits showed that fertilization had taken place and that the drop was due to some other cause. In many instances it was undoubtedly due to overproduction, as the tree was too small to bring to full maturity all the fruits that set. Pollination of the flowers on the same tree in 1909, according to the theory of pro-

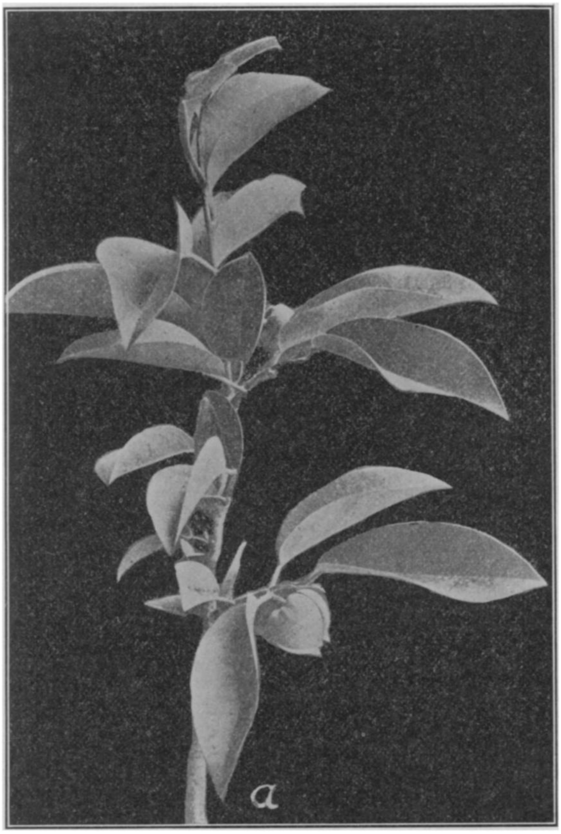

FIGURE 4. Pond apple flowers; a type introduced from Trinidad, B. W. I. (One third natural size.)

terogyny, produced another crop of fruits that year and the flowers responded likewise to pollination in the spring of 1910. Dr. A. Robertson Proschowsky, Nice, France, writes me that the results obtained by him in pollination experiments conducted on the cherimoya are analogous to those obtained by the author.

The plants of the sugar apple and the custard apple available for experimentation bore a larger number of flowers than the one cherimoya plant, and 143 flowers on one sugar apple tree were, in April and May, 1908, pollinated with their own pollen or that of flowers of other plants of the same species, 41 with pollen of the cherimoya, 41 with pollen of the pond apple, and 51 flowers with pollen from the custard apple. In no instance did fruit set where the pollen was applied to the stigma simultaneously with the discharge of its pollen; practically all responded where it was applied fifteen to forty-eight hours previous

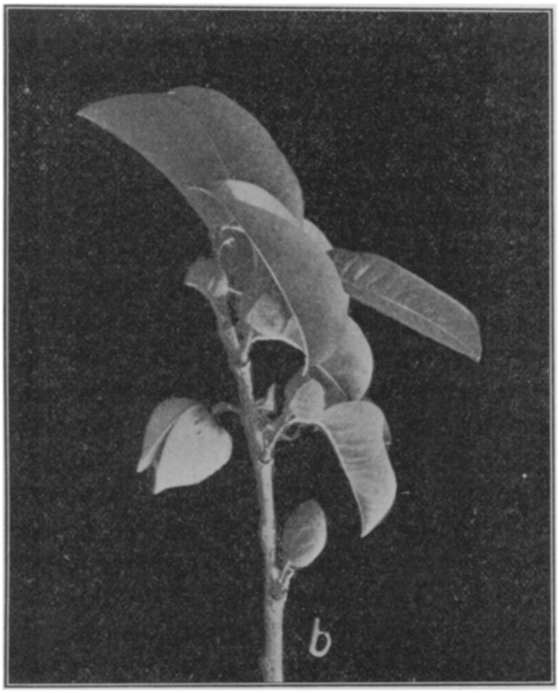

FIGURE 5. Pond apple flowers; a type indigenous to South Florida. (One third natural size.)

to this act, though here, as in the case of the cherimoya, the tree shed much of the fruit before it matured owing to its inability to carry it all. In September twenty-five pollinations of flowers on a sugar apple tree were made, in accordance with the theory of proterogyny, all successful. In order to verify the observations already made in regard to the pollinization and fertilization of the flowers of the species, over 100 flowers were pollinated on three trees in April and May, 1910, the results confirming the conclusions already made.

The pollination experiments with the custard apple in 1908 were conducted on three trees. In the course of these experiments 154 flowers, pollinated twenty-four hours before the discharge of the pollen in the flower, all, with few exceptions, set; 104 flowers, pollinated at the time of its discharge, all dropped.

The writer has in the course of his work with the Anonas in a very few instances noted that individual trees subjected to apparently the same conditions as others less fruitful were exceedingly prolific and from the results obtained in these investigations concluded that this was possibly due to synacmy and self-pollination. In order to obtain some information on this point with respect to the pond apple and to ascertain whether the pollination of the flowers of this species conformed to the same laws as those of its cultivated congeners, a series of experiments was carried through during April and May this year. Sixty-two flowers were bagged, in order to exclude all foreign pollen; none of these set. Fifty-six flowers were pollinated with pond apple pollen eighteen or more hours before the discharge of the pollen, and seven with pollen of the sugar apple and the cherimoya, with the result that sixty flowers were fecundated. The pollination of the flowers of this species thus appears to be analogous to that of its cultivated congeners.

The flowers of the pond apple, which belongs to the section *Guanabani* Martius, have six distinct, glabrous, concave, fleshy, outwardly yellowish white petals, in two series, the exterior being 25 to 40 mm. long, marked with red near the base inside, the interior smaller and red within except for a narrow transverse yellowish band near the base, the arrangements of the androecium and gynoecium being similar to those in the *Attae*. The flowers open sufficiently twenty-four hours before the shedding of the pollen to admit the entrance of small insects to the stigmas. Practically all the flowers shed their pollen early in the morning before sunrise; only rarely has it been noted in the afternoon. This is accompanied by a strong, rather disagreeable odor and it is highly probable that the pollination is performed by nocturnal insects. There is no evidence that the pollination of this species is performed in the manner indicated by Morong in *Anona cornifolia* St. Hil., the construction of whose flowers is very similar, and the results obtained in the pollination work show that the pollen must be conveyed from one flower to another in a less advanced stage of development.

In this connection it is interesting to note that the observations on *Anona cornifolia* St. Hil. in Paraguay by Morong, to which my attention was directed a few months ago, led him to the conclusion that this species also is entomophilous.

> "The stigmas lie . . . as far as I could judge entirely out of reach of the pollen by any action of the organs themselves. I found, however, that the pollen was very plentiful and that a pin thrust through the anthers obliquely would carry its grains to the stigmas. There seemed in the older flowers to be evidence that this operation is performed by insects, and I came to the conclusion that the plant must always depend for fructification upon insect agency."*

It would appear that Morong considered the stamens and pistils synchronous, although it is not evident that this conclusion was arrived at after investigation. That the flowers might have been dichogamous seemingly escaped him.

In the course of the pollination experiments of the cherimoya and custard apple a very interesting observation of the retardation of the development of a large number of fruits was made. Some cherimoya fruits developed without interruption from the time of pollination and matured in September, while a number remained stationary in size, about 8 mm. in diameter, until after July 25, when they suddenly began to increase in size and matured in October and November.

The flowering season of the custard apple begins in the latter half of May and continues throughout the summer and fall. Curiously enough, the flowers, which occur in great abundance, do not set until October and November, the fruit maturing in the spring. The pollination experiments with this species were started in May and continued during the following months. As already stated on a previous page, nearly all the pollinated flowers set, but with exceedingly few exceptions remained stationary in size, 6–8 mm. in diameter, until November, when they started to develop and matured in the usual season. The few fruits whose development began immediately after the pollination of the flowers matured in December.

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*Morong, T. Ann. N. Y. Acad. Sci. 7: 47. 1892.

The investigations indicate that the flowers of the cherimoya, the sugar apple, the custard apple, and the pond apple are proterogynous and entomophilous, though the pollinating agent of the last-named species has not been detected.

Since the investigations here related began, the cherimoya, after the trees have grown larger, has without artificial pollination, though sparingly, set fruit in Florida less than 20 feet above tide water. In California and Southern France it likewise fruits at a low altitude. In some parts of the world, *i. e.*, Hawaii, the species fruits only at an elevation of many hundred feet above the sea level. On investigation it may be found that this is due to the presence there of certain insects that do not occur at lower altitudes.

The sterility of the cherimoya in Florida has undoubtedly been due to the scarcity of blooms, which on this species is only one third of the number on the sugar apple, and to an insufficient number of insects to assist in the pollination of the flowers. As the trees grow larger and carry a greater number of flowers they may be expected to fruit more abundantly.

It has been demonstrated that the sugar apple hybridizes readily with the cherimoya, custard apple, and pond apple; the cherimoya has also been successfully crossed with the pond apple. So far, the attempts to cross the soursop, *Anona muricata* L., with the cherimoya, sugar apple, and custard apple have failed.

The extraordinary productivity of a few individual trees suggests a change in regard to the pollination of the flowers of these trees, possibly due to synacmy and self-pollination. Should this hypothesis be confirmed on investigation, such trees would be of inestimable value for breeding work in the creation of varieties that are independent of outside agencies for fructification.

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